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A comparison of the vegetation of forested and non-forested solution dolines in Hungary: a preliminary study

Zoltán Bátori[1]*, Tünde Farkas[2], László Erdős[1], Csaba Tölgyesi[1], László Körmöczi[1] & András Vojtkó[3]

[1] *University of Szeged, Department of Ecology, H-6726 Szeged, Közép fasor 52, Hungary; e-mail: zbatory@gmail.com*
[2] *Directorate of the Aggtelek National Park, H-3758 Jósvafő, Tengerszem oldal 1, Hungary*
[3] *Eszterházy Károly College, Department of Botany, H-3300 Eger, Leányka utca 6, Hungary*

Abstract: The present study compares the vegetation characteristics of two large forested and one large non-forested solution dolines in Hungary. We investigated the species composition and vegetation pattern along north to south transects (across the doline bottoms) and compared the richness of different species groups (dry and wet groups) on the doline slopes. We applied linear regression models for each slope to explore the effects of topography on species richness, and Detrended Correspondence Analysis (DCA) to detect the major gradients of floristic variation within each site. We found that the vegetation changed significantly along all transects; and, regardless of the vegetation cover, the doline bottoms contained several cool-adapted species. Variations within the two species groups were more pronounced on the south-facing slopes. The changes were similar in the forested dolines, indicating the role of forest cover in maintaining many cool-adapted species on the north-facing slopes as well. However, the number of cool-adapted species increased significantly along both slopes of the non-forested doline from the upper edge to the bottom. Contrary to our expectations, the species turnover along the slopes of the non-forested doline was lower than that along the slopes of the forested ones. We conclude that both the forested and non-forested dolines serve as refuges for many plant species adapted to different environmental conditions. Apart from providing an understanding of population patterns along environmental gradients, our results may also contribute to our understanding of an even more fundamental question for a future research agenda: the probable effects of climate change on vegetation characteristics in climatic islands with environmental conditions substantially different from the surrounding areas.

Key words: climate change; karst surface; refugium; relict species; species turnover

Introduction

Karst dolines, i.e., small to large depressions, are among the most interesting objects of karst surfaces. Since their total area may be relatively large in karst landscapes, they influence ecological processes considerably.

As isolated or semi-isolated cool and humid enclaves, dolines are very important from a nature conservation point of view. It has been shown that such depressions are refugia for a variety of species (Beck v. Mannagetta 1906; Horvat 1953; Vilisics et al. 2011). As our previous studies revealed (Bátori et al. 2012; 2014a), the role of the large and deep forested solution dolines of Hungary in plant species preservation is especially important. These studies also establish that the slope of species-area curves of dolines may change markedly depending on which species group is under consideration. For example, the slope of species-area curve is relatively low in the case of widespread species, which occur all over on the karst surfaces, and tends to be steeper if cool-adapted species are considered only. The literature contains many excellent examples where dolines are mentioned as key habitats for rare and endangered plant species (e.g., endemic, mountain, high mountain, marsh, relict and wet-woodland species) (Egli 1991; Vojtkó 1994; Yannitsaros et al. 1996; Dakskobler et al. 2008; Bátori et al. 2009; Lazarević et al. 2009). The most important species belong to the group of climatic relicts (e.g., *Dracocephalum ruyschiana* or *Stachys alpina* in Hungary) (Bartha 1933; Bátori et al. 2012), whose populations persist in isolated or semi-isolated enclaves of suitable climate space surrounded by areas where the climate is not suitable for them (Hampe & Jump 2011). The microclimate of dolines represents steep gradients (Gargano et al. 2010; Bátori et al. 2011), which has a profound influence on vegetation composition and results in a great diversity within short distances (Özkan et. al 2010). Temperature inversion and increased soil moisture lead to an inversion of vegetation zones (e.g., mesic beech forests replace dry oak forests on the deeper slopes of dolines) or to the development of edaphic vegetation types (e.g. scree and

* Corresponding author

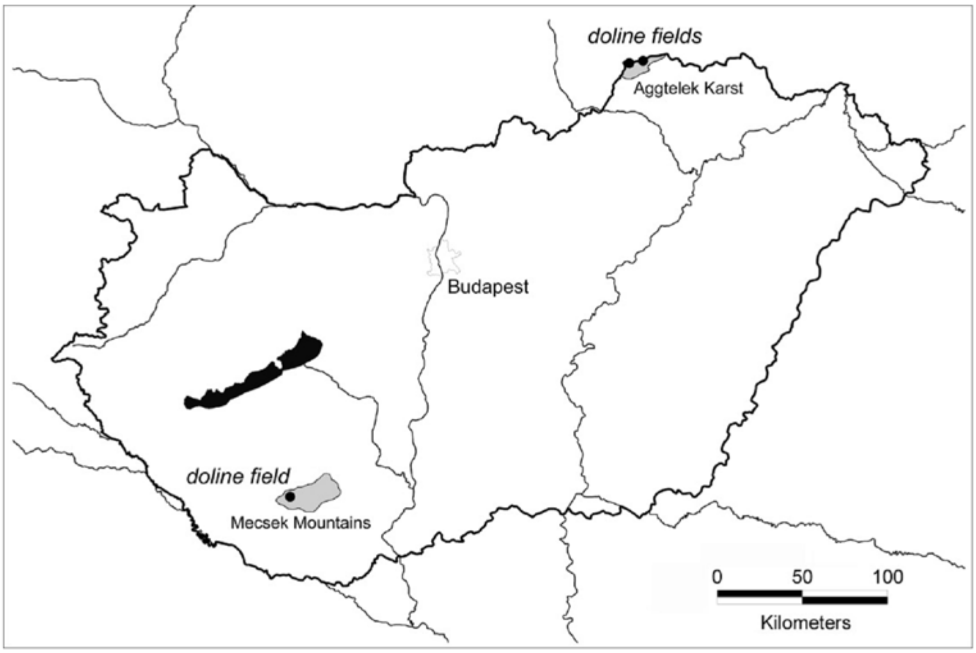


Fig. 1. Location of the study sites in Hungary.

ravine forests) (Horvat 1953; Vojtkó 2003; Bátori et al. 2014a). Sometimes dolines serve as refuges for endemic associations as well (Redžić et al 2011).

As the above-mentioned examples suggest, understanding the interactions among microclimate, topography and vegetation is the key to protecting the biodiversity of dolines and their surroundings. There is no doubt that the strength of temperature inversion, which is influenced predominantly by the topography, has a great impact on plant survival. However, vegetation cover can also have its share in influencing the temporal and spatial variability of temperature in dolines, mainly by modulating the intensity of solar insolation on doline slope surfaces. As previous studies have shown, microclimatic values are usually less extreme in forested dolines than in dolines covered with herbaceous or shrubby vegetation (Bacsó & Zólyomi 1934; Lehmann 1970). Nevertheless, the spring and autumn temperature variability and extremes in forested dolines may have a significant impact on the preservation and recolonization of cool-adapted species.

In this article, we present and discuss data demonstrating that in the studied forested and non-forested solution dolines many vegetation characteristics show spatial patterns that are interrelated, and such interrelationships contribute to species preservation following local topography. Moreover, we aimed to assess whether forest cover would suppress changes in vegetation characteristics along doline slopes.

Material and methods

Study sites

The fieldwork was carried out during the summer of 2007, 2012 and 2013 in three large and deep solution dolines, which can be considered typical for the karst areas of Hungary between 300 and 500 m a.s.l.

One forested doline (doline 1) was selected in the Mecsek Mountains (southern Hungary) and one non-forested (doline 2) and one forested doline (doline 3) in the Aggtelek Karst region (northern Hungary) (Figs 1, 2). Large and deep non-forested dolines are absent in the Mecsek Mountains.

All dolines had a similar topography (diameter is between 120 m and 150 m and depth is between 15 m and 20 m).

The average annual precipitation of the Mecsek Mountains, where doline 1 is located, is about 700 mm. Due to the sub-Mediterranean climate, the annual maximum values occur during the summer and autumn months. The annual mean temperature is about 9.5 °C (Marosi & Somogyi 1990). This doline is situated in the oak-hornbeam belt of the mountain range, in the mosaics of Illyrian type oak-hornbeam (*Asperulo taurinae-Carpinetum*) and beech forests (*Helleboro odori-Fagetum*).

The average annual precipitation of the Aggtelek Karst region is about 650 mm with the annual maximum during summer months. Annual mean temperature is about 9.1 °C (Ujvárosy 1998). Due to the continental climate, winters are colder than in the Mecsek Mountains. Doline 2 is surrounded by semi-dry grasslands (*Polygalo majori-Brachypodietum pinnati*) and doline 3 by Central European type oak-hornbeam forests (*Carici pilosae-Carpinetum*).

Vegetation sampling

Transects for sampling the herb layer were established across the dolines in north to south direction, traversing their deepest points. Each transect consisted of a series of 1 m × 1 m plots spaced at 5 m intervals. At all sites, we recorded presence/absence data of herbaceous plants and tree saplings in each square meter. A total of 86 plots were recorded.

Plant community names were used according to Borhidi et al. (2012), while the names of plant species followed Király (2009). Red-listed plants were identified according to Király (2007).

Fig. 2. An oak-hornbeam forest (*Asperulo taurinae–Carpinetum*) on the rim of doline 1 (A); a semi-dry grassland (*Polygalo majori–Brachypodietum pinnati*) and a montane hay meadow (*Anthyllido–Festucetum rubrae*) in doline 2 (B); a scree forest (*Mercuriali-Tilietum*) in doline 3 (C). Photos by Tünde Farkas and Zoltán Bátori.

Species grouping
All vascular plant species recorded along the transects were classified according to their coenological preferences using the classification of Soó (1980) and field observations. Two groups of species were established for each doline. The first group (hereafter called 'dry group') contains species which are associated with drier soil conditions and warmer climate (*Quercion farnetto*, *Quercetea pubescentis-petraeae* and *Querco-Fagetea* in doline 1; *Cirsio-Brachypodion*, *Festucetalia valesiacae*, *Festucion rupicolae*, *Festuco-Brometea* and *Quercetea pubescentis-petraeae* in doline 2; *Quercetea pubescentis-petraeae* and *Querco-Fagetea* in doline 3) and the second group (hereafter called 'wet group') contains species characteristic of moister soil conditions and cooler climate (i.e., cool-adapted species) (*Alnetea glutinosae*, *Atropion bella-donnae*, *Calystegion sepium*, *Fagetalia sylvaticae*, *Fagion illyricum* and *Tilio-Acerion* in doline 1; *Arrhenatheretea*, *Fagetalia sylvaticae*, *Molinio-Arrhenatheretea*, *Molinio-Juncetea*, *Nardetalia*, *Nardo-Callunetea*, *Pino-Quercetalia*, *Querco-Fagetea* and *Tilio-Acerion* in doline 2; *Galio-Alliarion* and *Fagetalia sylvaticae* in doline 3).

Statistical analyses
Linear regression analysis was used to evaluate the species richness–slope position relationships for both the dry and wet groups along each doline slope. The significance level was chosen $P < 0.05$. One-way ANOVA and subsequent Tukey's HSD post hoc tests were applied in order to reveal the differences in species richness between the sites.

Boundary delineation along the transects was done using the moving split-window (MSW) technique (Webster 1978; Bátori et al. 2014a) and field observations.

Detrended Correspondence Analysis (DCA) was used to detect the major gradients of floristic variation of the plots within the study sites (Hill & Gauch 1980).

Calculations were performed using Past 2.15 (Hammer et al. 2001). The MSW-computations were performed using the statistical language R 2.10.1 (R Development Core Team 2009).

Results

We detected 40, 128, and 43 species along the transects in doline 1, doline 2 and doline 3, respectively (Figs 3–5). Species compositions changed markedly along the transects. Some species occured in every part of the dolines (e.g., *Fraxinus excelsior*, *Hedera helix* and *Viola reichenbachiana* in doline 1; *Cirsium pannonicum*, *Festuca rupicola* and *Salvia pratensis* in doline 2; *Fraxinus excelsior*, *Galium odoratum* and *Viola reichenbachiana* in doline 3), while others were restricted to only the south-facing slopes (e.g., *Carpinus betulus*, *Carex flacca* and *Dactylis polygama* in doline 1; *Chamaecytisus albus*, *Pulsatilla grandis* and *Sanguisorba minor* in doline 2; *Acer campestre*, *Carex montana* and *Crataegus monogyna* in doline 3), to the north-facing slopes (e.g., *Euonymus europaeus*; *Lathyrus venetus* and *Mercurialis perennis* in doline 1; *Convallaria majalis*, *Galium schultesii* and *Gentiana cruciata* in doline 2; *Daphne mezereum*, *Dryopteris filix-mas* and *Fagus sylvatica* in

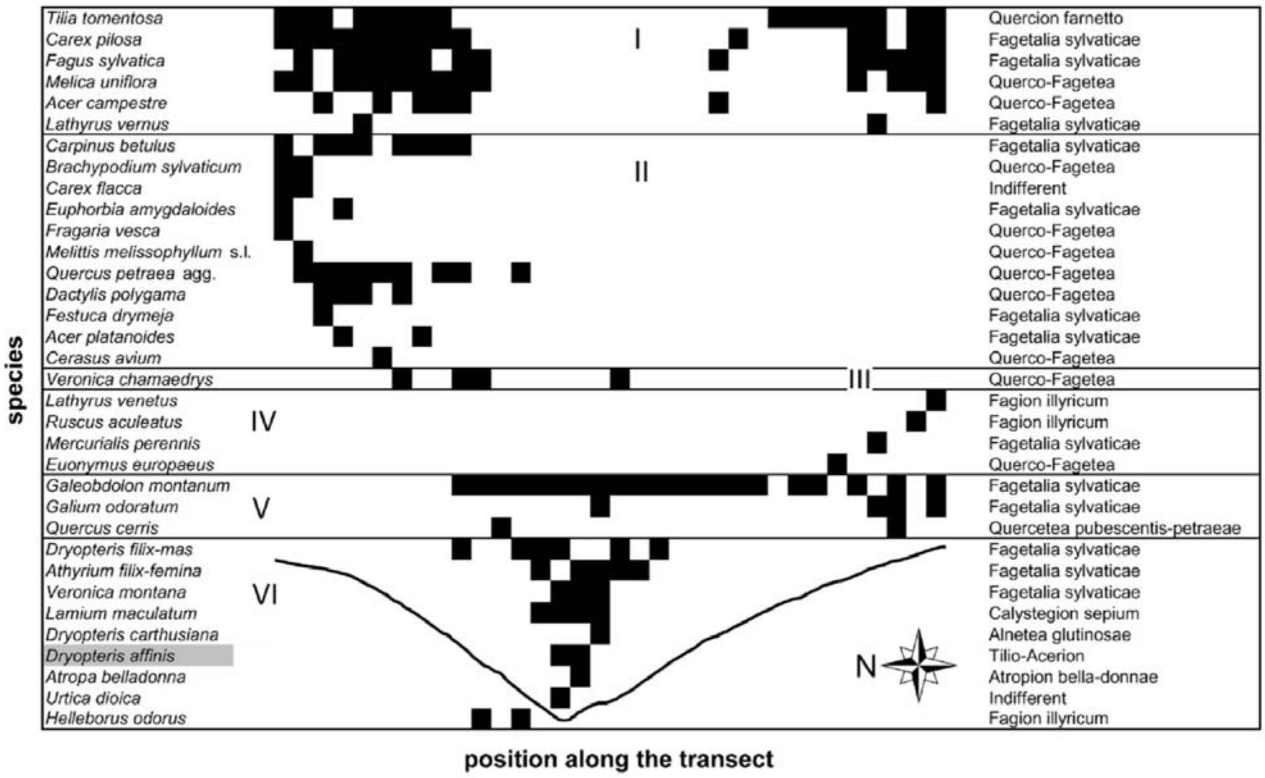


Fig. 3. Species occurrences and relief profile along the transect of doline 1. I – species of the rims and upper slopes; II – species of the south-facing slope; III – species of the south-facing slope and doline bottom; IV – species of the north-facing slope; V – species of the north-facing slope and doline bottom; VI – species of the doline bottom. Those species that occur in every part (I–VI) of the doline transect include *Ruscus hypoglossum* (*Fagion illyricum*), *Acer pseudoplatanus*, *Hedera helix*, *Rubus hirtus* agg., *Viola reichenbachiana* (*Fagetalia sylvaticae*) and *Fraxinus excelsior* (*Querco-Fagetea*). The name of the red-listed plant is grey-shaded.

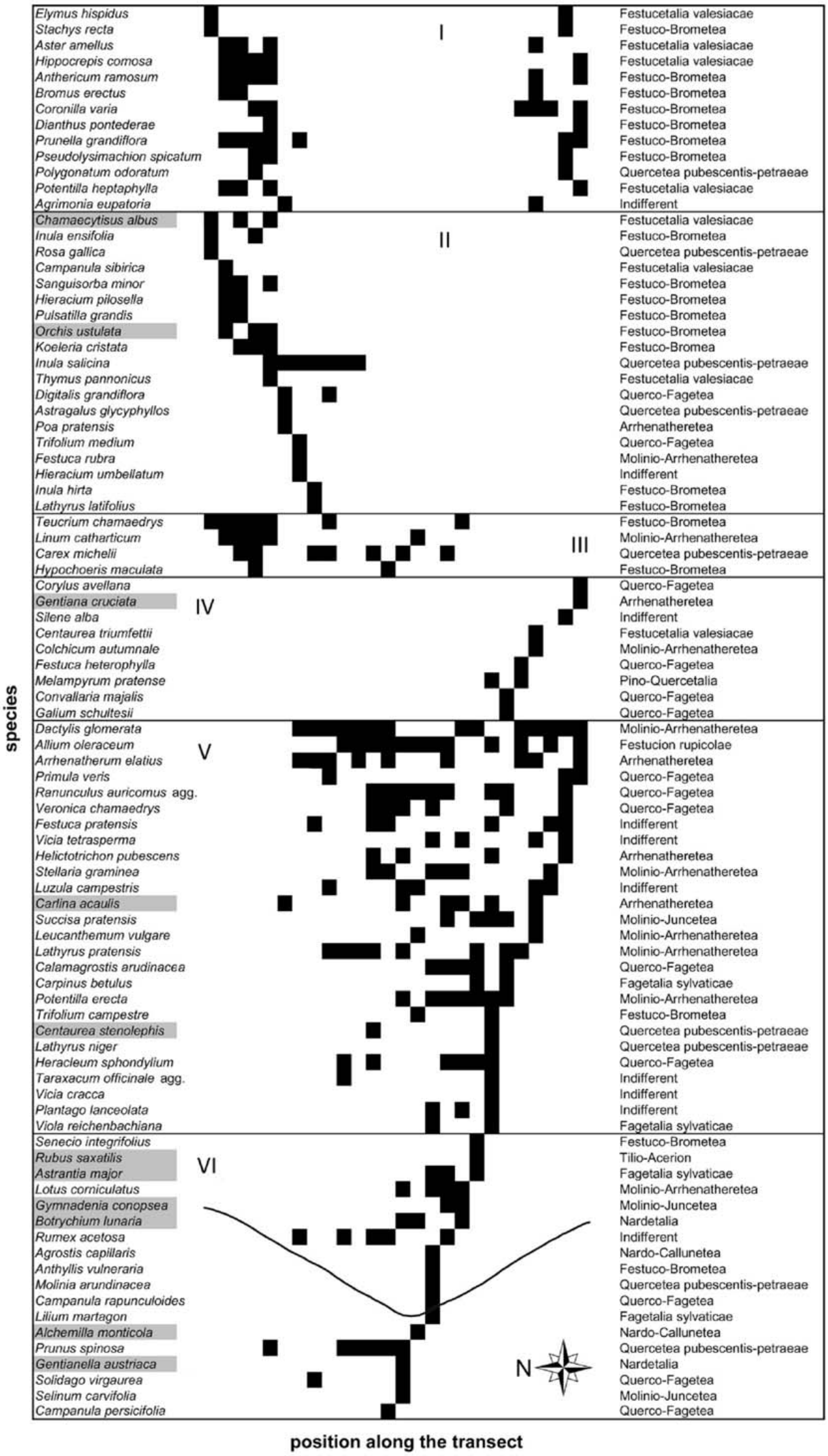
doline 3) or to the doline bottoms (e.g., *Dryopteris affinis*, *Urtica dioica* and *Veronica montana* in doline 1; *Agrostis capillaris*, *Alchemilla monticola* and *Botrychium lunaria* in doline 2; *Paris quadrifolia*, *Urtica dioica* and *Stellaria media* in doline 3). Most of the red-listed plants (e.g., *Astrantia major*, *Daphne mezereum* and *Gentianella austriaca*) were found on the north-facing slopes or in the doline bottoms. Some of them (e.g., *Rubus saxatilis*) are very rare in Hungary. The proportion of the red-listed plants was the highest (8.6%) in doline 2.

The species richness of the dry group decreased toward the doline bottom both on the south-facing and the north-facing slopes of doline 1 and doline 3, and on the south-facing slope of doline 2, while the species richness of the wet group showed the reverse distribution on both slopes of doline 2 (Fig. 6). However, in the case of the wet group of doline 1 and doline 3, significant correlation could only be detected along the south-facing slopes.

However, if we consider only the individual coenological groups, for example *Fagetalia sylvaticae*, we can expect a more precise pattern of species occurrences and related ecological processes (Figs 3–5). *Querco-Fagetea* species were frequent on the rims and south-facing slopes of doline 1 and doline 3, while *Fagetalia sylvaticae* species dominated (i.e., their proportion was higher) mainly the lower slopes and doline bottoms. Ravine forest species (*Tilio-Acerion*), wet woodland species (*Alnetea glutinosae*) and natural weed species (*Atropion bella-donnae*, *Calystegion sepium* and *Galio-Alliarion*) occurred only on the doline bottoms. More coenological groups could be distinguished in doline 2. Dry grassland species (*Festucetalia valesiacae* and *Festuco-Brometea*) dominated the rims and the south-facing slope, hay meadow species (*Molinio-Arrhenatheretea*) and mesic forest species (*Querco-Fagetea*) the north-facing slope, while ravine forest species (*Tilio-Acerion*) and species of nutrient-poor habitats (*Nardetalia* and *Nardo-Callunetea*) occured only in the doline bottom.

Doline 2 proved to be much richer in species ($P < 0.001$) than doline 1 and doline 3, which, in turn, showed no significant difference ($P = 0.915$) regarding species richness (Fig. 7). The DCA ordinations of the samples show a strong gradient along axis 1 with a high species turnover in doline 1 (eigenvalue: 0.63, gradient length: 4.4 S.D. units) and in doline 3 (eigenvalue: 0.65, gradient length: 5.2 S.D. units) and lower species turnover along the slopes of doline 2 (eigenvalue: 0.42, gradient length: 3.1 S.D. units) (Figs 8–10).

More than one vegetation type was detected along all transects. On the north-facing rim of doline 1 a transitional forest stand occurred, composed of elements of turkey oak-sessile oak forests (*Potentillo micranthae-Quercetum dalechampii*) and oak-hornbeam forests(*Asperulo taurinae-Carpinetum*). The south-facing and north-facing slopes of the same do-


species
position along the transect
I
II
III
IV
V
VI
N
Elymus hispidus
Stachys recta
Aster amellus
Hippocrepis comosa
Anthericum ramosum
Bromus erectus
Coronilla varia
Dianthus pontederae
Prunella grandiflora
Pseudolysimachion spicatum
Polygonatum odoratum
Potentilla heptaphylla
Agrimonia eupatoria
Chamaecytisus albus
Inula ensifolia
Rosa gallica
Campanula sibirica
Sanguisorba minor
Hieracium pilosella
Pulsatilla grandis
Orchis ustulata
Koeleria cristata
Inula salicina
Thymus pannonicus
Digitalis grandiflora
Astragalus glycyphyllos
Poa pratensis
Trifolium medium
Festuca rubra
Hieracium umbellatum
Inula hirta
Lathyrus latifolius
Teucrium chamaedrys
Linum catharticum
Carex michelii
Hypochoeris maculata
Corylus avellana
Gentiana cruciata
Silene alba
Centaurea triumfettii
Colchicum autumnale
Festuca heterophylla
Melampyrum pratense
Convallaria majalis
Galium schultesii
Dactylis glomerata
Allium oleraceum
Arrhenatherum elatius
Primula veris
Ranunculus auricomus agg.
Veronica chamaedrys
Festuca pratensis
Vicia tetrasperma
Helictotrichon pubescens
Stellaria graminea
Luzula campestris
Carlina acaulis
Succisa pratensis
Leucanthemum vulgare
Lathyrus pratensis
Calamagrostis arudinacea
Carpinus betulus
Potentilla erecta
Trifolium campestre
Centaurea stenolephis
Lathyrus niger
Heracleum sphondylium
Taraxacum officinale agg.
Vicia cracca
Plantago lanceolata
Viola reichenbachiana
Senecio integrifolius
Rubus saxatilis
Astrantia major
Lotus corniculatus
Gymnadenia conopsea
Botrychium lunaria
Rumex acetosa
Agrostis capillaris
Anthyllis vulneraria
Molinia arundinacea
Campanula rapunculoides
Lilium martagon
Alchemilla monticola
Prunus spinosa
Gentianella austriaca
Solidago virgaurea
Selinum carvifolia
Campanula persicifolia
Festucetalia valesiacae
Festuco-Brometea
Festucetalia valesiacae
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Quercetea pubescentis-petraeae
Festucetalia valesiacae
Indifferent
Festucetalia valesiacae
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Quercetea pubescentis-petraeae
Festucetalia valesiacae
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Quercetea pubescentis-petraeae
Festuco-Brometea
Querco-Fagetea
Arrhenatheretea
Indifferent
Festucetalia valesiacae
Molinio-Arrhenatheretea
Querco-Fagetea
Pino-Quercetalia
Querco-Fagetea
Querco-Fagetea
Molinio-Arrhenatheretea
Festucion rupicolae
Arrhenatheretea
Querco-Fagetea
Querco-Fagetea
Querco-Fagetea
Indifferent
Indifferent
Arrhenatheretea
Molinio-Arrhenatheretea
Indifferent
Arrhenatheretea
Molinio-Juncetea
Molinio-Arrhenatheretea
Molinio-Arrhenatheretea
Querco-Fagetea
Fagetalia sylvaticae
Molinio-Arrhenatheretea
Festuco-Brometea
Quercetea pubescentis-petraeae
Quercetea pubescentis-petraeae
Querco-Fagetea
Indifferent
Indifferent
Indifferent
Fagetalia sylvaticae
Festuco-Brometea
Tilio-Acerion
Fagetalia sylvaticae
Molinio-Arrhenatheretea
Molinio-Juncetea
Nardetalia
Indifferent
Nardo-Callunetea
Festuco-Brometea
Quercetea pubescentis-petraeae
Querco-Fagetea
Fagetalia sylvaticae
Nardo-Callunetea
Quercetea pubescentis-petraeae
Nardetalia
Querco-Fagetea
Molinio-Juncetea
Querco-Fagetea

Fig. 4. Species occurrences and relief profile along the transect of doline 2. I – species of the rims and upper slopes; II – species of the south-facing slope; III – species of the south-facing slope and doline bottom; IV – species of the north-facing slope; V – species of the north-facing slope and doline bottom; VI – species of the doline bottom. Those species that occur in every part (I–VI) of the doline transect include *Briza media* (Arrhenatheretea), *Cirsium pannonicum* (*Cirsio-Brachypodion*), *Fragaria viridis*, *Polygala major*, *Trifolium alpestre* (*Festucetalia valesiacae*), *Asperula cynanchica*, *Brachypodium pinnatum*, *Euphorbia cyparissias*, *Festuca rupicola*, *Filipendula vulgaris*, *Geranium sanguineum*, *Helianthemum ovatum*, *Helictotrichon adsurgens*, *Phleum phleoides*, *Plantago media*, *Ranunculus polyanthemos*, *Salvia pratensis*, *Seseli annuum*, *Thesium linophyllon*, *Trifolium montanum*, *Trinia glauca* (*Festuco-Brometea*), *Achillea collina*, *Galium verum*, *Hypericum perforatum*, *Knautia arvensis*, *Leontodon hispidus*, *Pimpinella saxifraga* (Indifferent), *Serratula tinctoria* (*Molinio-Juncetea*), *Cruciata glabra*, *Symphytum tuberosum*, *Tanacetum corymbosum* (*Querco-Fagetea*) and *Betonica officinalis*, *Carex montana*, *Genista tinctoria*, *Peucedanum cervaria*, *Potentilla alba*, *Pulmonaria mollissima*, *Trifolium pannonicum*, *Viola hirta* (*Quercetea pubescentis-petraeae*). The names of the red-listed plants are grey-shaded.

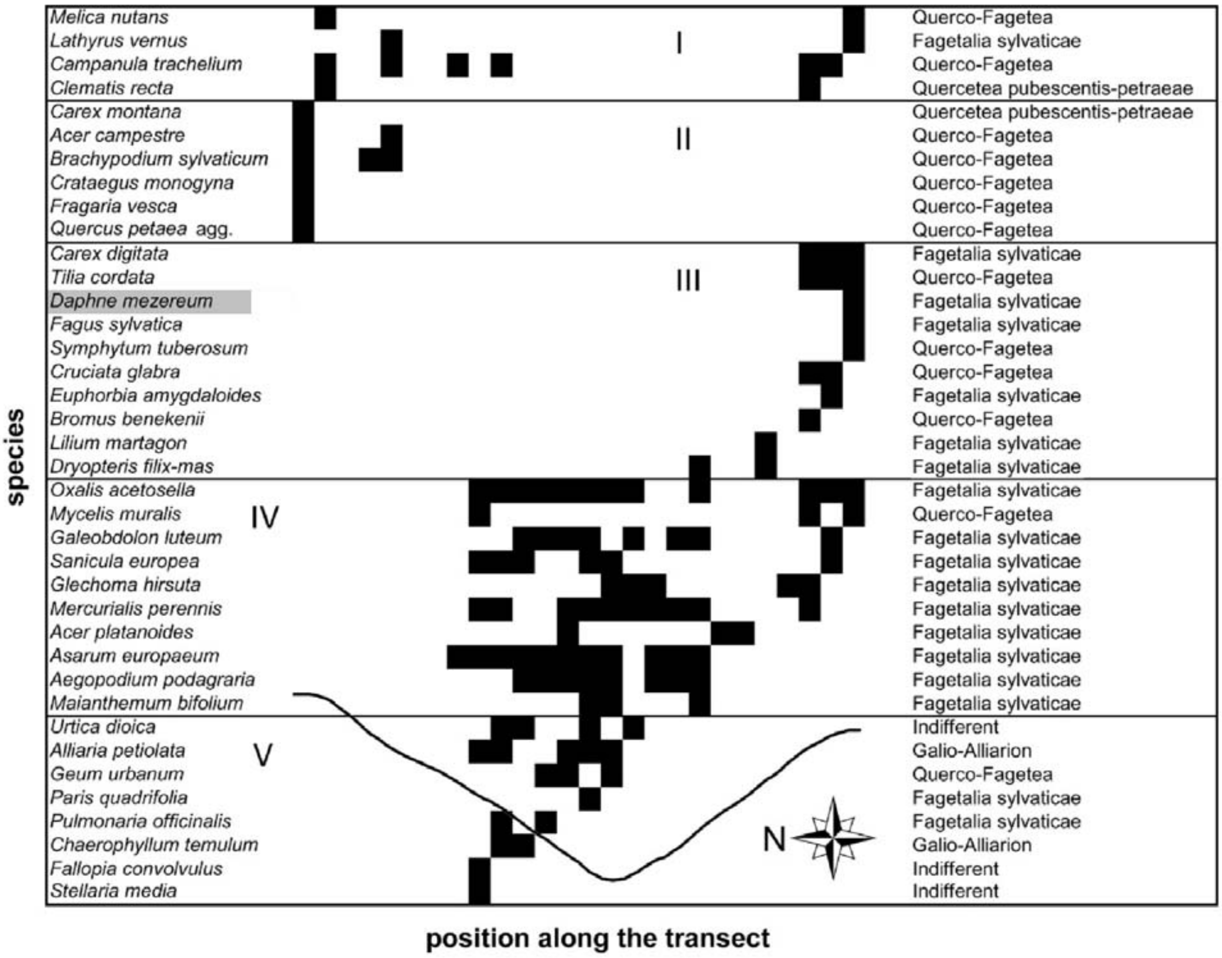

Fig. 5. Species occurrences and relief profile along the transect of doline 3. I – species of the rims and upper slopes; II – species of the south-facing slope; III – species of the north-facing slope; IV – species of the north-facing slope and doline bottom; V – species of the doline bottom. Those species that occur in every part (I–V) of the doline transect include *Acer pseudoplatanus*, *Carpinus betulus*, *Galium odoratum*, *Viola reichenbachiana* (*Fagetalia sylvaticae*) and *Fraxinus excelsior* (*Querco-Fagetea*). The name of the red-listed plant is grey-shaded.

line were occupied by an oak-hornbeam forest, whereas a ravine forest (*Scutellario altissimae-Aceretum*) patch occurred in the doline bottom. In doline 2, a semi-dry grassland (*Polygalo majori-Brachypodietum pinnati*) covered the rims and slopes, and a montane hay meadow (*Anthyllido-Festucetum rubrae*) the doline bottom. An oak-hornbeam forest (*Carici pilosae-Carpinetum*) was located on the upper slopes and rims of doline 3, while a scree forest (*Mercuriali-Tilietum*) in the doline bottom.

Discussion

We studied the species composition and vegetation pattern of forested and non-forested solution dolines in Hungary. Our results show that these dolines serve as refuges for many species adapted to very different climatic conditions. In addition, we revealed that vegetation inversion has developed independently of the vegetation cover. However, we found differences in species richness and species turnover, depending on the exposure and vegetation cover.

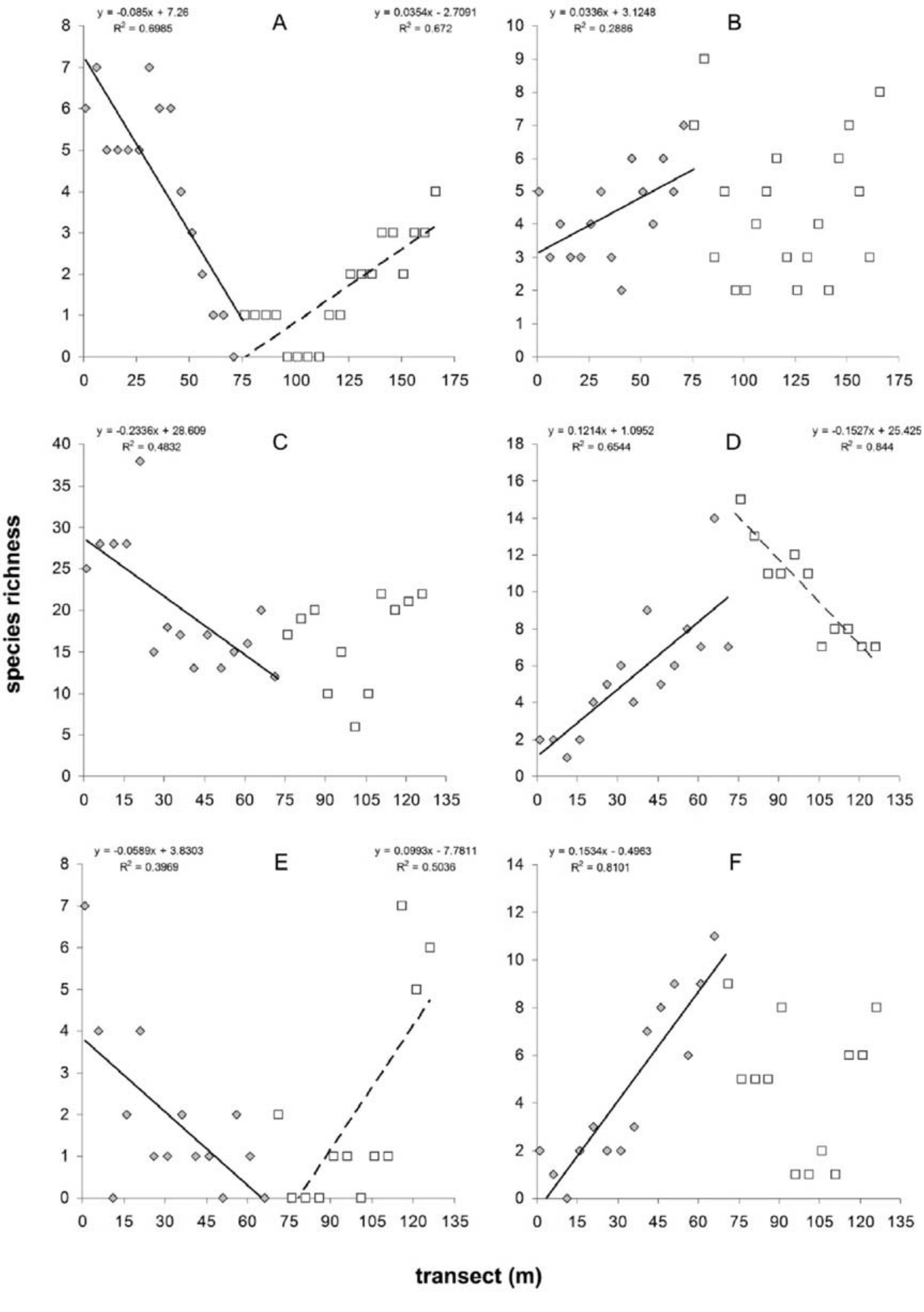

Fig. 6. The relationship between species richness and doline topography (i.e. position along the transect) in solution dolines of Hungary. A – dry group in doline 1; B – wet group in doline 1; C – dry group in doline 2; D – wet group in doline 2; E – dry group in doline 3; F – wet group in doline 3.

Understanding the patterns of doline vegetation requires an understanding of the spatial and temporal patterns of microclimate (Whiteman et al. 2004; Antonić et al. 2007). The interaction between topography and climate is very complex and its details are not completely understood (Dobrowski 2011). There is no doubt, however, that topography and related terrain effects strongly affect the local climatic conditions (Bátori et al. 2009; Geiger 1950; Whiteman et al. 2004) and therefore the species composition and vegetation

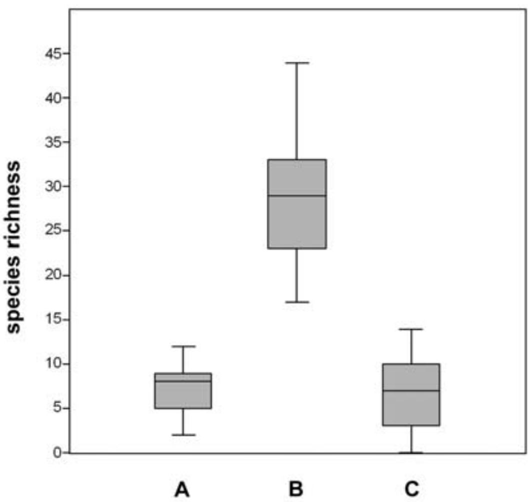

Fig. 7. Species richness of the three dolines studied. A – doline 1; B – doline 2; C – doline 3.

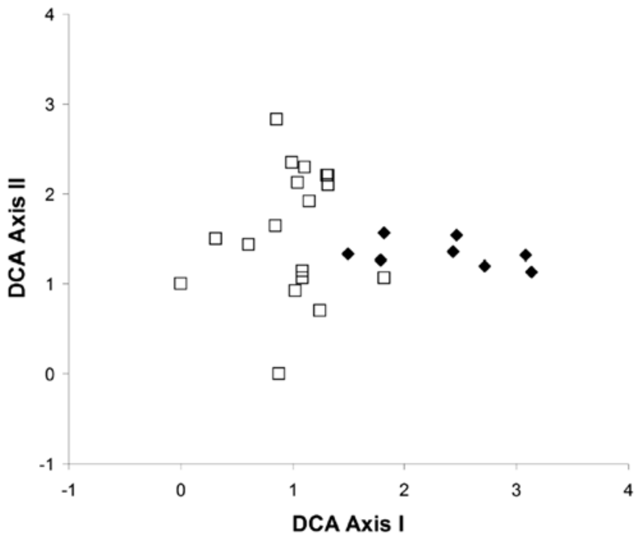

Fig. 9. DCA ordination scattergram of the 26 plots of doline 2. Eigenvalues of the first two axes were 0.4121 and 0.2687, respectively. ◆: *Polygalo majori-Brachypodietum pinnati*; □: *Anthyllido-Festucetum rubrae*.

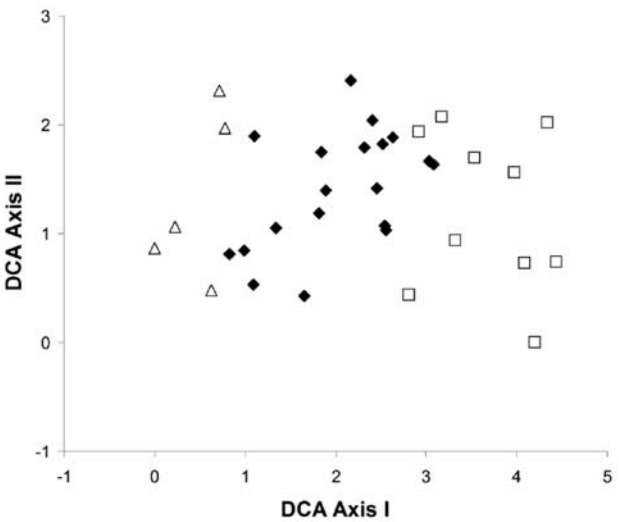

Fig. 8. DCA ordination scattergram of the 34 plots of doline 1. Eigenvalues of the first two axes were 0.6183 and 0.2392, respectively. △: transitional forest stand (*Potentillo micranthae-Quercetum dalechampii* and *Asperulo taurinae-Carpinetum*); ◆: *Asperulo taurinae-Carpinetum*; □: *Scutellario altissimae-Aceretum*.

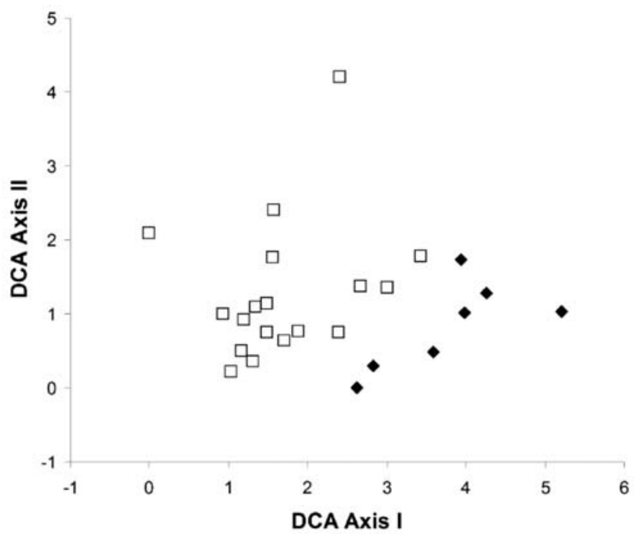

Fig. 10. DCA ordination scattergram of the 26 plots of doline 3. Eigenvalues of the first two axes were 0.6526 and 0.4185, respectively. ◆: *Carici pilosae-Carpinetum*; □: *Mercuriali-Tilietum*.

pattern. At night, a cold air lake builds up in the dolines, significantly determining the ecological processes on the slopes (Bárány-Kevei 1999). In an early study (Bacsó & Zólyomi 1934) revealed that the microclimate of dolines covered with grasslands may be very extreme and the average, minimum and maximum temperature values change markedly depending on which doline parts are considered. Similar results are shown by Lehmann (1970), who compared the microclimate of two large dolines, one of which was covered with mesic forests and the other one with a forest clear-cut. The two dolines differed considerably concerning air humidity and temperature regimes (air humidity changed between 95% and 100% while the temperature changed between 18 ℃ and 25 ℃ in the forested doline, while these values changed between 50% and 100% and 10 ℃ and 32 ℃ in the clear-cut doline).

Recent studies (Bátori et al. 2011, 2012) discuss the potential role of forested dolines in mitigating species loss under future global warming and conclude that these depressions may play an essential role in reducing extinction rate of plant species, as they did in earlier geological times as well (Horvat 1953). However, species preservation depends on many factors. Bátori et al. (2014a) emphasize that the types of dolines, the steepness of the slopes, the latitude and the vegetation history have a major impact on plant growth and survival. For example, when considering only solution dolines with similar depth/diameter ratio, larger dolines can be considered better refugia for plants than smaller ones. Our results revealed that all vegetation types found on the deeper slopes of the dolines and in the doline bottoms contain many plants that usually occur at higher elevations or in otherwise cool and moist habitats. Thus, we can conclude that not only the forested (Bátori et al. 2012, 2014a) but also the non-forested dolines play an important role in the preservation of vascular plant species in Hungary, and this phenomenon is attributed to the presence of specific environmental gradients. Presumably, the high-mountain and relict species of the studied dolines would survive for a long time under climate change.

We also found that variation within the dry and the wet species groups is more pronounced on the south-facing doline slopes. In Hungary, the south-facing slopes receive much more solar radiation than the north-facing ones, therefore the south-facing doline parts are warmer than the opposite ones (Jakucs 1971). Our results are in good agreement with the findings of other authors who found significant differences between the vegetation characteristics of north-facing and south-facing slopes in several environments (Hutchins et al. 1976; Armesto & Martínez, 1978; Hicks & Frank 1984; Kutiel & Lavee 1999; Erdős et al. 2012). The strong increase in species richness within the wet group along the north-facing slope of the non-forested doline can probably be explained by steep nighttime temperature gradients. However, the high number of cool-adapted species on the north-facing slopes of the forested dolines may primarily be related to the mitigating effect of the forest on temperature regime (Bátori et al. 2014b).

In contrast with our expectations, the species turnover is higher in the forested dolines. However, changes of the species richness of the wet group along the transects are pronounced only in the non-forested doline. At least two explanations of this apparent contradiction are possible. Firstly, the forest associations found in both areas (*Asperulo taurinae-Carpinetum*, *Carici pilosae-Carpinetum*, *Helleboro odori-Fagetum*, *Mercuriali-Tilietum* and *Scutellario altissimae-Aceretum*) are relatively rich in beech forest species (*Fagetalia sylvaticae*) (Jakucs & Jurko 1967; Kevey 1997; Kevey & Borhidi 1998; Nagy 2004), which have successfully colonized the cool north-facing slopes of the forested dolines as well. However, if we consider only the occurrences of individual species, we can conclude that there is a strong spatial separation between species of *Fagetalia sylvaticae* along the slopes of the forested dolines (presumably following soil moisture changes), strongly contributing to the high species turnover. For example, *Lathyrus vernus* occurs on the upper slopes of the dolines but it is absent from the bottoms. Secondly, several historical events (e.g. grazing and mowing regimes) might shape the vegetation pattern along the slopes of the non-forested doline and might contribute to the homogenization of the vegetation (Bárány-Kevei 1998).

Our results suggest that the forest cover exerts a major impact on species richness and species turnover in karst dolines and does not influence the phenomena of species preservation and vegetation inversion. We can conclude that the karst dolines of Hungary can be considered as potential refugia for many vascular plants under future global warming and are thus very valuable from a nature conservation point of view. Future investigations are necessary to develop our understanding of the relationships between vegetation cover and different vegetation characteristics in karst dolines in relation to altitude, regional climate and slope exposure.

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